

## EXTREMELY LOW NESTING SUCCESS AND CHARACTERISTICS OF LIFE HISTORY TRAITS IN AN INSULAR POPULATION OF *PARUS VARIUS NAMIYEI*

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**ABSTRACT.**—Differing intensities of predation pressure can affect the evolution of life history traits in island and mainland populations. We found extremely low nesting success in an insular subspecies of the Varied Tit (*Parus varius namiyei*; Kozushima Island), and we compared certain life history traits among three subspecies of *P. varius* experiencing different predation pressures. The nesting success of *P. v. namiyei* was extremely low as a result of significant nest predation and nest abandonment; 83% of active nests failed due to snake predation. The proportion of depredated nests was significantly greater on Kozushima Island than on Miyakejima Island (*P. v. owstoni*) or on the mainland (*P. v. varius*). Of the three subspecies, *P. v. namiyei* had the longest incubation period, shortest nestling period, an intermediate clutch size, and a small brood size. There were no differences in the date of egg laying among the three populations. The short nestling period for *P. v. namiyei* may be an adaptive response, as the predation risk during the nestling period on Kozushima was extremely high. Received 3 August 2004, accepted 16 March 2005.

Nest predation is a major cause of nestling mortality in avian species (Ricklefs 1969, Skutch 1985, Martin 1988, Rotenberry and Wiens 1989, Weatherhead and Blouin-Demers 2004). The intensity of predation pressure can affect the evolution of life history traits (Cody 1971, Clark and Wilson 1981, Slagsvold 1982, Nilsson 1984, Stutchbury and Morton 2001), and high nest predation generally results in selection for individuals that can reduce their investment in each breeding attempt (Slagsvold 1982, Lundberg 1985). This is particularly true of small birds, which are usually unable to protect their nests against predators. Some researchers have investigated this theory by comparing island and mainland populations, because predation pressure on islands often differs from that of mainland populations (Higuchi 1976, Loiselle and Hoppes 1983, George 1987, Sieving 1992). Higuchi (1976) reported that some life history traits of one insular subspecies of the Varied Tit (*Parus varius owstoni*) differed from those of the mainland subspecies (*P. v. varius*) and that predation pressure differed between the two populations.

We report extremely low nesting success in one insular subspecies (*P. v. namiyei*) of the Varied Tit and compare certain life history traits with those of two populations studied by Higuchi (1976), each of which is subjected to different predation pressure. We also discuss whether the differences in predation pressure could be responsible for the variation in life history traits among three different subspecies of Varied Tits.

### METHODS

*P. varius* occurs on the Japanese mainland and islands, the southern Korean Peninsula, and Taiwan. The species is divided into eight subspecies across its range (Ornithological Society of Japan 2000). *P. v. varius* occurs on the mainland of Japan and the southern Korean Peninsula, *P. v. namiyei* is found on three northern islands (Nijijima, Toshima, and Kozushima; Fig. 1) of the Izu Archipelago, and *P. v. owstoni* occurs on three southern islands (Miyake, Mikura, and Hachijo).

**Study site.**—The study site was Kozushima Island, Tokyo, Japan (18.87 km<sup>2</sup>; 34° 12' N, 139° 08' E; population ~2,100). The island is part of Fuji-Hakone-Izu National Park, but has a residential area that occupies about 10% of the island. The dominant vegetation is broad-leaved evergreen forest, mostly *Castanopsis cuspidate*, *Machilus thunbergii*, and second-growth *Abus sieboldiana*. Patches of cedar (*Cryptomeria japonica*) plantations are interspersed throughout the island. The climate is

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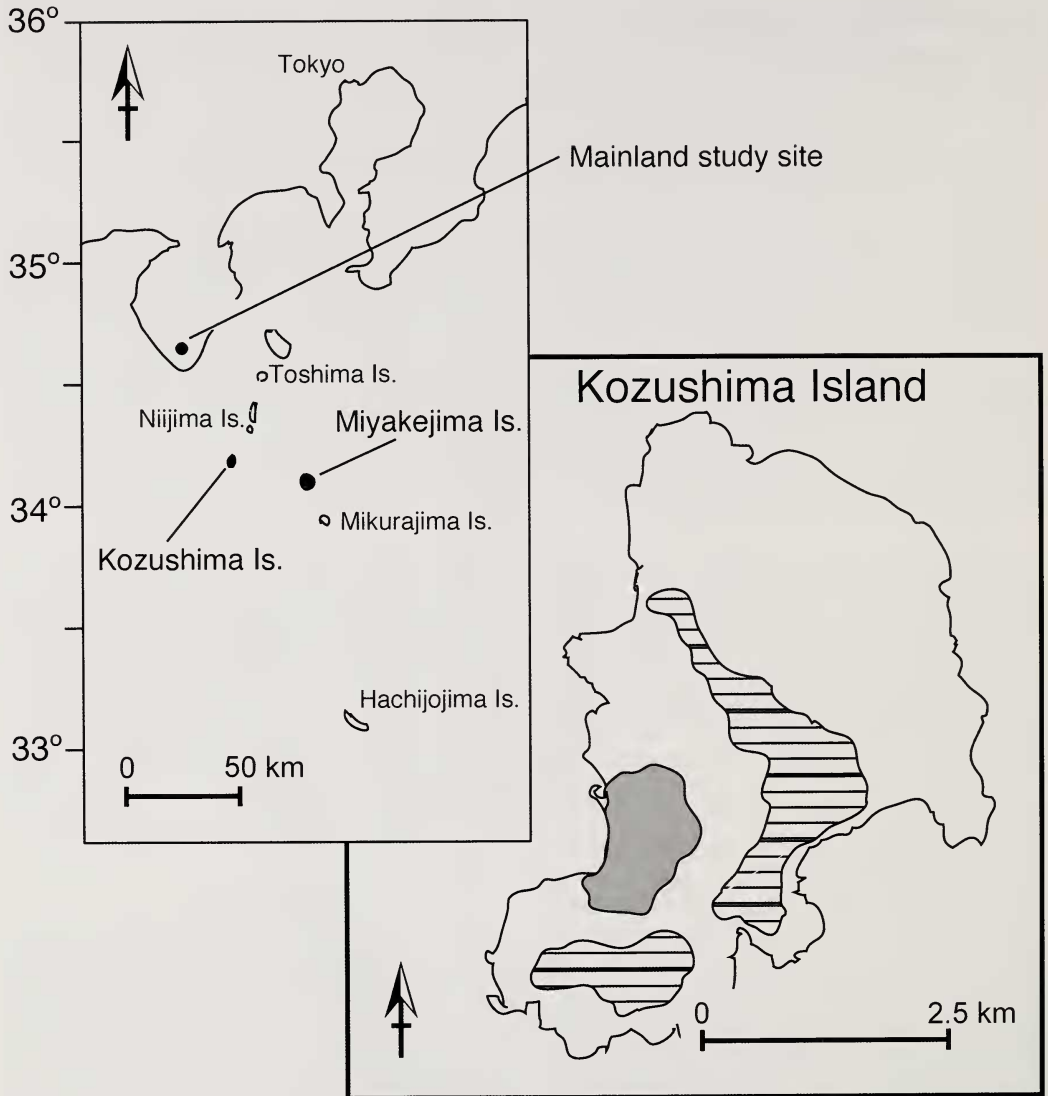


FIG. 1. Map of the Izu Archipelago and adjacent mainland of Japan, showing locations of the study sites described in both this paper and in a prior study (Higuchi 1976). The gray and hatched areas on Kozushima Island indicate the residential area and the approximate locations where nest boxes were placed, respectively.

temperate, with a mean annual rainfall of 2,535 mm and a mean annual temperature of 17.4° C. Mean temperature and rainfall on Miyakejima Island and the adjacent mainland are 16.5° C, 1,832 mm and 17.5° C, 2,907 mm, respectively (Japan Meteorological Agency, [www.jma.go.jp/JMA\\_HP/jma/indexe.html](http://www.jma.go.jp/JMA_HP/jma/indexe.html)).

*Field observations.*—We erected 137 nest boxes in 2003 and 136 boxes in 2004 (122 × 122 × 180; cavity entrance = 34 mm). Boxes were attached at a height of 2.5 m to 4–6-m

tall broad-leaved evergreen trees and 6–10-m tall planted Japanese cedars throughout the island, with the exception of the residential area and extremely steep areas. The distance between boxes was approximately 50 m. We checked each box every 3 days and recorded status, laying date, clutch size, hatching date, number of unhatched eggs, brood size, and fledging date. Our estimates of fledging date thus had a maximum possible error of 3 days; hatching date was adjusted according to de-

velopment of nestlings. We categorized predation as follows: if neither the box nor the nesting material had been damaged or disturbed, we concluded that the predator was a snake; if the entrance hole was enlarged and encircled with peck marks, we concluded that the predator was a bird (probably the Jungle Crow, *Corvus macrorhynchos*). Small, mammalian nest predators, such as martens, weasels, and squirrels, do not inhabit the island. Successful nests were defined as those from which at least one young fledged. In total, 99 of 273 boxes were used (at least one egg was laid). We attached a baffle under 48 of the 99 boxes to prevent predation by snakes; the data obtained from these boxes were excluded from calculations of predation frequency (i.e., 51 nests were used in the analyses).

*Statistical analyses.*—We calculated daily nest survival rates using the maximum likelihood method (Johnson 1979). Daily nest survival rates for the egg and nestling stages were analyzed separately. The egg period was defined as the time between the date the first egg was laid until at least one egg hatched; we defined the nestling period as the time between hatching of the first egg and fledging (Cresswell 1997). To compare daily survival rates, we used Z-tests according to the methods outlined by Johnson (1979).

Using multiple, two-tailed *t*-tests, we compared predation rates and life history traits of *P. v. namiyei* on Kozushima Island to those reported for *P. v. owstoni* and *P. varius* by Higuchi (1976) on Miyakejima Island and the mainland, respectively. We assumed that variables of life history traits followed *t* distributions, and used two-tailed Welch's *t*-tests when comparing life history traits among the three populations. We did not use ANOVA because we wanted to compare life history traits only between the Kozushima population and the other populations, and, moreover, because the variance values for all four life history traits greatly differed among populations (clutch size:  $\chi^2 = 12.05$ ,  $df = 2$ ,  $P = 0.002$ ; brood size:  $\chi^2 = 23.78$ ,  $df = 2$ ,  $P < 0.001$ ; incubation period:  $\chi^2 = 116.61$ ,  $df = 2$ ,  $P < 0.001$ ; nestling period:  $\chi^2 = 15.82$ ,  $df = 2$ ,  $P < 0.001$ ). Probability values were adjusted using sequential Bonferroni methods (Ury 1976, Sokal and Rohlf 1995). The familywise error rate was calculated as  $\alpha = 1 - (1 - 0.05)^{18}$ ,

where *k* is the number of tests. Adjusted *P*-values were calculated as  $P_{adj} = (0.05/\alpha) \times P$ . To compare the proportion of depredated nests, we used Fisher's exact test. We analyzed data using the software package R 1.8.1 (<http://cran.r-project.org/>).

## RESULTS

*P. v. namiyei* used 99 of 273 nest boxes (72/137 in 2003 and 27/136 in 2004); 51 of the 99 nests were used in the analyses (see Methods). Nest success (7.84%) of *P. v. namiyei* was extremely low on Kozushima Island due to nest predation and nest abandonment. Four nests were successful, 18 (35.29%) were abandoned, 19 (37.25%) were depredated, 5 (9.8%) failed because of human disturbance, and 1 (2.0%) failed due to deterioration. Four nests (7.84%) failed due to unknown causes (perhaps disease or starvation). Excluding inactive nests (abandoned, disturbed, and unknown), 82.6% (19 of 23) of active nests were depredated, all by snakes. We determined the predator species by direct observation in nine cases; all were Japanese rat snakes (*Elaphe climacophora*). Predation on a given nest was always complete (100%). Daily survival probabilities during the egg and nestling stages were  $0.991 \pm 0.002$  SE and  $0.891 \pm 0.034$  SE, respectively. The daily survival probability during the nestling stage was significantly lower than that during the egg stage ( $Z = 2.91$ ,  $P = 0.002$ ). The probability that a nest would survive through the egg and nestling stages was 0.835 (=  $0.991^{19.98}$ ) and 0.148 (=  $0.891^{16.57}$ ), respectively (Table 1).

We compared the predation pressure on Kozushima Island (*P. v. namiyei*) with that on the mainland (*P. v. varius*) and on Miyakejima Island (*P. v. owstoni*; Table 1). The proportion of depredated nests was higher on Kozushima (0.37) than on Miyakejima (0.00) or on the mainland (0.30; Fisher's exact test: Kozu versus Miyake,  $P < 0.001$ ; Kozu versus mainland,  $P < 0.001$ ). We also compared several life history traits of *P. v. namiyei*, *P. v. varius*, and *P. v. owstoni* (Table 1). *P. v. namiyei* exhibited the longest incubation period (*namiyei* versus *varius*,  $P < 0.001$ ; *namiyei* versus *owstoni*,  $P = 0.001$ ), the shortest nestling period (*namiyei* versus *varius*,  $P = 0.008$ ; *namiyei* versus *owstoni*,  $P < 0.001$ ), an intermediate clutch size (*namiyei* versus *varius*,  $P < 0.001$ ;

TABLE 1. Predation pressure (percent depredated nests) and life history traits of *P. v. namiyei* on Kozushima Island, *P. v. varius* on the mainland, and *P. v. owstoni* on Miyakejima Island, Japan. Data for the mainland and Miyakejima are from Higuchi (1976). Standard errors of the brood size for the mainland and Miyakejima are original data by HH. Mean values  $\pm$  standard errors are shown. Figures in parentheses are sample sizes.

Traits	Kozushima	Miyakejima	Mainland
Predation pressure (%)	37.25 (51)	0.00 (46)	30.28 (109)
Incubation period (days)	15.56 $\pm$ 0.22 (34)	14.06 $\pm$ 0.03 (42)	13.95 $\pm$ 0.09 (87)
Nestling period (days)	16.57 $\pm$ 0.40 (14)	18.76 $\pm$ 0.20 (39)	18.23 $\pm$ 0.27 (71)
Clutch size	5.42 $\pm$ 0.13 (76)	3.92 $\pm$ 0.10 (52)	6.23 $\pm$ 0.08 (101)
Brood size	4.33 $\pm$ 0.19 (51)	3.78 $\pm$ 0.31 (46)	6.05 $\pm$ 0.13 (76)

*namiyei* versus *owstoni*,  $P < 0.001$ ), and a small brood size (*namiyei* versus *varius*,  $P < 0.001$ ; *namiyei* versus *owstoni*,  $P = 0.14$ ).

### DISCUSSION

The nesting success of *P. v. namiyei* on Kozushima was extremely low as a result of high levels of nest predation and nest abandonment; 83% of active nests were depredated. In all cases, the predators were snakes, probably Japanese rat snakes. We frequently found these snakes when checking nest boxes, and although no abundance data are available, we consider them to be abundant on Kozushima.

The proportion of abandoned nests was also large (0.35). Significant predation pressure may result in a relatively low threshold of tolerance before a female *P. v. namiyei* will abandon her nest. Nest abandonment and re-nesting induced by nest predation are likely subjected to strong selective pressure; thus, any decision rule may be adaptive (Bauchau and Seinen 1997). We believe that our regular nest checks did not induce abandonment. Nest abandonment rates due to human disturbance (12%) in our study were not as high as those reported in other studies of *P. varius* (15%; Yamaguchi and Kawano 2001, Yamaguchi et al. 2003).

Predation rates differed between Kozushima, Miyakejima, and the mainland, although the sites are relatively similar in terms of vegetation and climate. The differences in predation rates are probably a function of the differences in snake abundance. Snakes are absent from Miyakejima Island, and no nest predation was observed by Higuchi (1976). Japanese rat snakes are native to both Kozushima Island and the mainland.

The three subspecies of *P. varius* differed in terms of their life history traits. The nest-

ling period of *P. v. namiyei* was the shortest among the three populations. This result supports the notion that high predation levels may exert strong selection pressure on length of nestling period (Skutch 1949, Cody 1966, Lack 1968, Andersson et al. 1980, Milonoff 1989, but see Barash 1975). This may be an adaptive response, as the predation risk during the nestling stage on Kozushima Island was extremely high. The shorter nestling period in *P. v. namiyei* may be due, in part, to a relatively small brood size (Slagsvold 1984, Bosque and Bosque 1995) or more rapid growth during the nestling phase.

Of the three subspecies, *P. v. namiyei* had the longest incubation period, and its clutch size was intermediate. These life history traits would seem to be maladaptive under the influence of high predation pressure, as birds can reduce their investment in any one breeding attempt by reducing clutch size (Perrins 1977, Ricklefs 1969, Slagsvold 1982, Lundberg 1985). However, prolonged incubation periods and undiminished clutch sizes may be related to low hatchability in *P. v. namiyei* (K. Fujita unpubl. data), which could be attributable to low nest attentiveness at crucial periods during the embryo development period.

Differences in life history traits among populations evolve in response to a number of ecological and environmental factors (e.g., longevity, mating system, food abundance, climate, and predation pressure). Of these factors, predation pressure may be one of the most important factors producing the observed differences in life history traits in the subspecies of the Varied Tit.

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